Foraging Recruitment by the Giant Tropical Ant, *Paraponera clavata* (Hymenoptera, Formicidae)

BRUCE A. BARRETT,[1] CLIVE D. JORGENSEN, AND SANDRA J. LOOMAN

Department of Zoology, Brigham Young University, Provo, Utah 84602.

Increased foraging of an exceptionally abundant, but ephemeral, food source by ants can result from foraging excitement that does not include pheromone trails, tandem running, or from recruitment of other workers along pheromone trails (Carrol and Janzen, 1973). They also provided rationale for two types of short-lived pheromone trails resulting in mass or group recruitment. These both seem to fall into the Type II foraging strategy described by Oster and Wilson (1978). Neither of these discussions conveniently allow for pheromone recruitment by relatively small colonies of a primitive monomorphic species such as *Paraponera clavata*. Our observations suggest that recruitment to an abundant ephemeral food source does occur naturally and can be induced artificially in colonies of *P. clavata*.

Paraponera clavata is considered primitive (Wilson, 1958), particularly in foraging habits (Young and Hermann, 1980; Young, 1977). Hermann (1973, 1975) reported that *P. clavata,* unlike more advanced species, forages independently; following short periods of apparent group activity outside of the colony (Young and Hermann, 1980). It reportedly does not return to a food source when only part has been harvested. After returning to its colony with booty, a single worker resumes foraging independently, with no observable tendency to return to partially harvested booty or without recruiting additional workers to collect the remaining food (Hermann, 1973; Young and Hermann, 1980). Reports of independent foraging, lack of forager recruitment, and apparent lack of food source fidelity resulted in the assumption that *P. clavata* probably lacks an effective pheromone trail communication system (Young and Hermann, 1980).

METHODS

Five colonies of *P. clavata* on Barro Colorado Island, Panama, were selected for our studies. All entrances to the colonies were positioned at the bases of trees, with other trees, shrubs and vines within 1 m of the entrance. Ants foraging from each colony were observed continuously for 24 hr to determine when foraging activity was lowest and to assess which possible foraging routes were not used. These routes were marked for subsequent placement of an artificial food source (sugar-water in a plastic bag equipped with a sponge wick). Food sources were located on unused limbs or vines about 4 m from the frequently used routes, but always in contact with them via interconnecting vines, limbs, etc. The food sources were each placed about 2 m above the ground surface.

Tests were conducted at four colonies to determine if recruitment to a food

[1] Present address: Department of Entomology, Washington State University, Pullman, Washington 99164.

Table 1. Average response times (min) of *Paraponera clavata* for recruitment and pheromone tests.

Response time of ants	Colonies			
	Lathrop 2	Lutz 1	Lutz 2	Lutz 3
Marked ant				
Spent at the food site	6.39	7.13	7.59	4.07
Spent in returning to nest	0.35	5.20	1.51	1.17
Number of returned visits to the food site	3.50	2.00	2.00	1.50
Unmarked ants				
Emerging from nest after marked ant first entered the nest	0.29	5.75	0.19	1.10
Spent in traveling on first visit to the food site	1.35	2.40	.056	1.41

source was evident and to determine if pheromone trails were established to aid the recruitment. The fifth colony was used as a control to observe non-induced foraging behavior. Tests were conducted from late morning to midday when natural foraging was least active. During these hours, the only persistent activity was mound workers excavating dirt and removing debris from the mound. Prior to starting each test, foraging activity was observed for 30 min after the sugar-water had been installed to make sure that it was not located by natural foragers.

One mound worker was placed directly on the sponge wick. After collecting sugar-water had started, the ants' thorax and abdomen were marked with white Liquid Paper® (Liquid Paper Corp., Box 61, Boston, MA 02199) for future identification. The following data were then recorded: (1) the time required for the marked ant to return to the colony entrance with sugar-water booty, (2) number of times the marked ant returned to the food source within 15 min after it was first placed on the source, (3) time interval between entrance into the colony by the marked ant and exit by an unmarked ant on its way to the food source, (4) time interval for the first unmarked ant to reach the food source and (5) the rate at which ants arrived at the food source.

These methods were also used to determine if trail pheromones were deposited, except all possible routes leading to the food source from the colony entrance were covered with leaves for these observations. After several ants had crossed over the leaves, allowing ample time for a pheromone trail to be established on the leaves, they were removed and all ants at the food source placed back at the colony entrance. Following this, the times required to relocate the food source and re-establish foraging trails were recorded.

RESULTS AND DISCUSSION

Ants were found foraging most frequently during the late afternoon to early evening, but continued less frequently through the night. Comparable observations were also reported by McClusky and Brown (1972). Because we timed our tests to coincide with the least active foraging periods, natural discovery of the artificial food sources did not occur.

A brief period of disoriented behavior by the mound worker placed on the artificial food source was followed by collecting sugar-water booty. After spending 4.07–7.59 min collecting a droplet of booty, they returned the 6.0–8.5 m to the
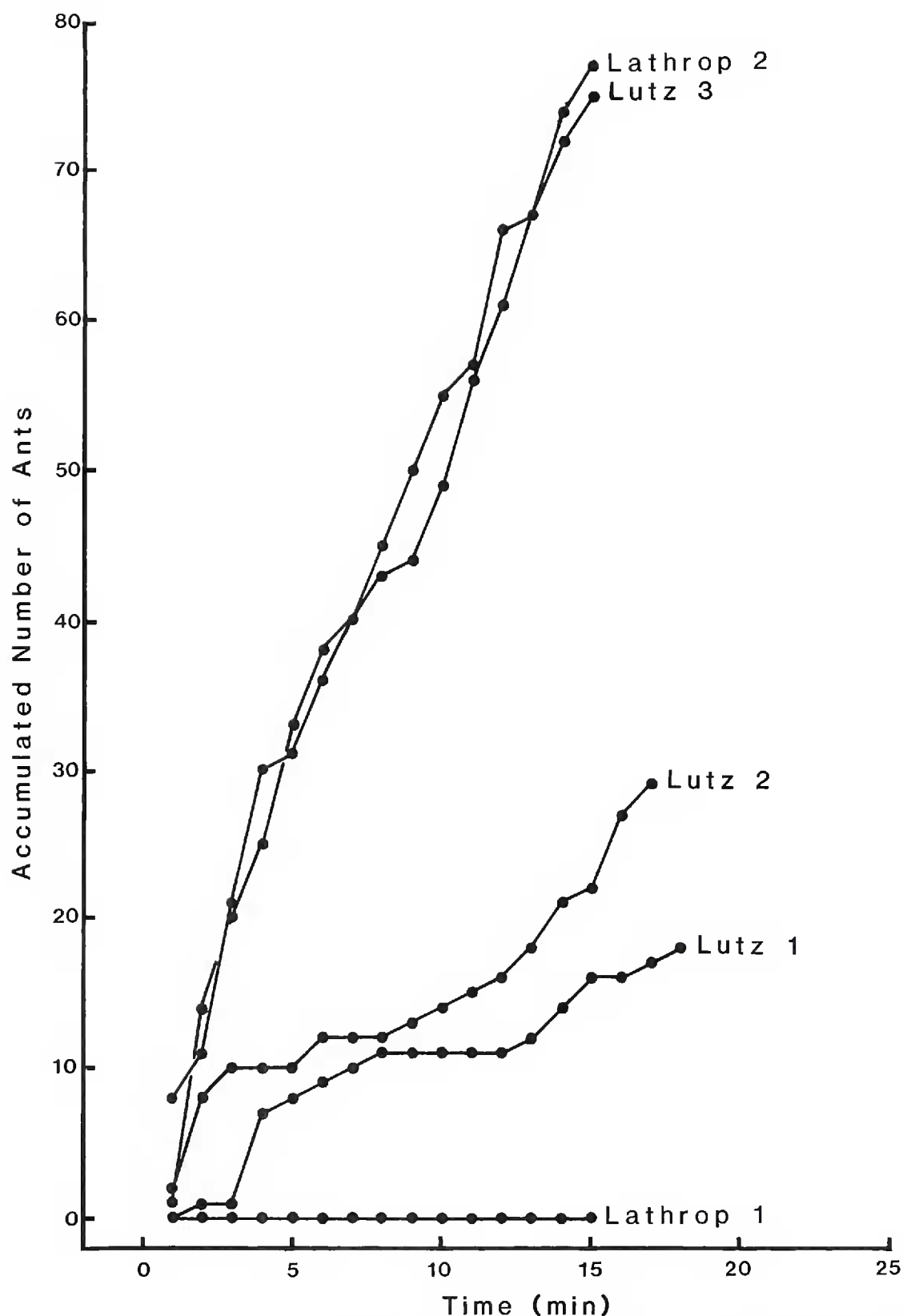
Figure 1. Cumulative visits of unmarked *Paraponera clavata* to the artificial food site after initial marked ant had returned to the nest after it had been introduced to the food site. Lathrop 1 is a control since a marked ant had not first been introduced to the food site.

colony entrance in 0.35–5.20 min (Table 1). Orientation to the entrance by the marked ants of each colony on their first return trips must have included some visual cues since its placement on the artificial food source precluded the possibility of a trail pheromone. What these visual cues were requires field experimentation with canopy and local vegetative characteristics. The use of visual cues to return while establishing pheromone trails has been reported for *Solenopsis saevissima* (Wilson, 1962) and is generally accepted as a functional phenomena for others (Carroll and Janzen, 1973).

Hermann (1973) reported that recruitment to a partially utilized food source

was not apparent for *P. clavata*. Our studies indicated active recruitment to the artificial food source, since in all but one case (Lutz 1), other ants within the colony reached the food source before the marked ant returned to it. This may not represent comparable behavior for naturally occurring food, but similar recruitment was apparent when ants from Lathrop 1 were observed collecting dozens of swarming termites that happened to land on the tree where the ant colony was located. In this case, the ants were very active (20+ ants at a time) in collecting the termites after the first forager returned to the colony entrance with its booty.

Effective recruitment to a food source requires a means of reliably communicating locations of the booty, usually some type of dance or pheromone (Carroll and Janzen, 1973). The marked ant was observed dragging its gaster while returning to the colony entrance the first time, suggesting the deposition of a trail pheromone. This behavior was not observed by the ant from the control colony that was placed on a branch without booty. Also, as the number of ants using the trail increased, the speed of movement along the trail appeared to increase. Orientation to the food source and colony entrance become more precise and movement more direct as the number of passages along the trail increased.

The number of ants recruited from each colony was variable since additional ants were recruited continuously throughout the observations in some colonies (Fig. 1, Lathrop 2 and Lutz 3), whereas others seemed to reach a limit of recruits (Fig. 1, Lutz 1 and 2), and the control had no recruitments (Fig. 1, Lathrop 1). Although one might speculate why such apparent differences occurred, without nutritional and colony population data, it would not likely be helpful to our basic understanding of their behavior.

The use of trail pheromones by *P. clavata* has not been reported (Hermann, 1973; Young and Hermann, 1980), although it apparently does possess the ability of maintaining foraging routes close to the nest (Hermann and Young, 1980). By eliminating the presumed pheromone trails when the leaves they were on were removed, we temporarily disrupted recruitment to the artificial food sources. Foraging behavior was apparently reduced to searching behavior when they encountered the interrupted trail. Additional observations need to be made to validate the presence and longevity of trail pheromones more completely.

Conclusions

Recruitment to an exceptional food source by *P. clavata* can be induced using sugar-water, and as reported for their attack on termites probably occurs more frequently under natural conditions than originally thought. Utilization of an abundant food source may be more effective than previously thought, since *P. clavata* workers did return to the food source several times (Table 1). Foragers following the same path established by an original marked ant indicates that trail pheromones probably play an important role in the foraging behavior of *P. clavata*.

Acknowledgments

Literature Cited

Carroll, C. R., and D. H. Janzen. 1973. Ecology and foraging by ants. Ann. Rev. Ecol. Syst., 4:231–147.

Hermann, H. R. 1973. Formation of preforage aggregations in ponerine ants (Hymenoptera: Formicidae), a possible step toward group raiding. J. Georgia Entomol. Soc., 8:185–186.

———. 1975. Crepuscular and nocturnal activities of *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). Entomol. News, 86:94–98.

———, and A. M. Young. 1980. Artificially elicited defensive behavior and reciprocal aggression in *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). J. Georgia Entomol. Soc., 14:8–10.

McCluskey, E. S., and W. L. Brown. 1972. Rhythms and other biology of the giant tropical ant *Paraponera*. Psyche, 79:335–347.

Oster, G. F., and E. O. Wilson. 1978. Caste and ecology in social insects. Princeton Univ. Press, 352 pp.

Young, A. M. 1977. Notes on the foraging of the giant tropical ant *Paraponera clavata* (Formicidae: Ponerinae) on two plants in tropical wet forest. J. Georgia Entomol. Soc., 12:41–51.

———, and H. R. Hermann. 1980. Notes on foraging of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). J. Kansas Entomol. Soc., 53:35–55.

Wilson, E. O. 1958. The beginnings of nomadic and group-predatory behavior in the ponerine ants. Evol., 12:24–36.

———. 1962. Chemical communication among workers of the fire ant *Soleopsis saevissima* (Fr. Smith). I. The orientation of mass foragers. Anim. Behav., 10:134–147.